Biology of the blue swimmer crab *Portunus pelagicus* in Leschenault Estuary and Koombana Bay, south-western Australia

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Abstract

The blue swimmer crab *Portunus pelagicus* was sampled monthly in Leschenault Estuary and the marine embayment (Koombana Bay) into which it opens. The trends exhibited by density and size-frequency data are consistent with those previously recorded for this portunid in this estuary, implying that the spawning period, the timing of immigration and emigration, and the pattern of growth are similar each year in Leschenault Estuary. The monthly trends exhibited by the numbers and prevalence of ovigerous female crabs, together with previous data on the distribution of crab zoea, provide strong circumstantial evidence that *P. pelagicus* typically release their presumptive zoea in Koombana Bay, rather than in Leschenault Estuary, and that this occurs predominantly in mid-spring to late summer. Although a few 0+ recruits enter the estuary in the ensuing months, their numbers do not start to rise markedly until the following mid-to late spring, when salinities and water temperatures in the estuary are rising appreciably. At this time, the carapace widths (CW) of the majority of these crabs lie between 40 and 100 mm. During the ensuing months, the corresponding cohort increases greatly in both numbers and body size, with the result that, by the completion of their first year of life in January, the CW of many of its females and males have reached 97 mm and 84 mm, respectively, the size at which 50% of the corresponding sexes of *P. pelagicus* undergo a pubertal moult. These and other data demonstrate that *P. pelagicus* first spawn when they are approximately one year old. Although the abundance of crabs in Leschenault Estuary rises during spring and summer, that of particularly the older crabs subsequently falls precipitously during the subsequent winter months and early spring, when the crabs are *ca* 18-20 months in age and salinities and water temperatures undergo a marked decline. The pronounced decline in the abundance of crabs in the estuary in winter and early spring is accompanied by a conspicuous rise in their numbers in the shallows of Koombana Bay, indicating that the crabs, which had emigrated from the estuary, had entered the alternative habitats provided by that embayment. A substantial number of crabs are found in Koombana Bay throughout the year. The sex ratios of crabs in samples collected by different methods indicate that females tend to leave the estuary before males and that crab pots have a greater tendency to catch male crabs than female crabs. The catch and catch per unit effort of the commercial fishery for *P. pelagicus* in Leschenault Estuary is greatest in January and February. This reflects in part the fact that, during these months, crabs are particularly abundant and are starting to attain the legal minimum size for capture (CW = 127 mm). This feature, together with the predominance of undersized crabs in earlier months and the emigration of crabs from the estuary in winter, help account for the marked seasonality of the fishery for this portunid in this estuary. Furthermore, as water temperatures are at their maxima in summer, the crabs are likely to be particularly active at this time and thus also most susceptible to capture. In the Leschenault Estuary, *P. pelagicus* feeds mainly on slow-moving or sessile macrobenthic invertebrates, such as amphipods, polychaetes, and bivalve and gastropod molluscs, and also occasionally on gobies, and thus in this system it can be regarded as essentially a benthic carnivore.

Keywords: Leschenault Estuary, *Portunus pelagicus*, size and age compositions, sex ratios, spawning, size at first maturity, recruitment, commercial fishery, south-western Australia.

Introduction

The Leschenault Estuary, which is located between latitudes 33° 12' S and 33° 20' S on the lower south-west coast of Australia, contains a large lagoonal-like basin, which is 14 km long and between 1.5 km and 2.5 km wide and in most regions is less than 2 m in depth (Semeniuk & Meagher 1981). The main tributary, the Collie River, discharges into the southernmost region of this basin, opposite the point where the entrance channel of the estuary opens into the sea at the northernmost end of Koombana Bay.

The blue swimmer crab *Portunus pelagicus* is found in waters throughout the Indo-West Pacific (Stephenson 1962), and is often sufficiently abundant to form the basis of a

substantial recreational and/or commercial fishery in some of the estuaries and coastal waters in that region, including those of Leschenault Estuary (*e.g.* Potter *et al.* 1983; Ingles & Braum 1989; Sumpton *et al.* 1989; Kailola *et al.* 1993; Jones & Morgan 1994; Sukumaran & Neelakantan 1996a). Meagher (1971) provided the first data on the biology of *P. pelagicus* in the Leschenault Estuary and Koombana Bay. He concluded that this portunid emigrates from the estuary into the bay in autumn and returns in spring, and that these movements are related to temperature differences between the estuary and the embayment. He also concluded that the females of *P. pelagicus* reach maturity within this estuary during their second year of life and then migrate out to sea, where the fertilised eggs are released and larval development occurs. Anon (1983), in contrast to Meagher (1971), concluded that (1) the migration of *P. pelagicus* into

Leschenault Estuary occurs in mid-summer rather than spring, (2) during the summer, a substantial number of blue swimmer crabs remain in Koombana Bay rather than entering the estuary and (3) the females of this portunid first breed during their first year of life rather than at the end of their second year of life. However, the studies of neither Meagher (1971) nor LeProvost *et al.* (1983) were carried out at frequent, regular (*i.e.* monthly) intervals in both Leschenault Estuary and Koombana Bay. Such frequent sampling is clearly required to resolve the conflicting views on the above aspects of the biology of *P. pelagicus* in these two water bodies

The aims of the present study were to sample both nearshore, shallow and offshore, deeper waters of Leschenault Estuary and Koombana Bay at monthly intervals over a protracted period to clarify the following: (1) the size composition and patterns of immigration, emigration and growth of *P. pelagicus* in Leschenault Estuary and the relationships between the trends exhibited by these variables and those displayed by salinity and water temperature, (2) the relationship between the assemblages of blue swimmer crabs in Leschenault Estuary and Koombana Bay, (3) the time of spawning and the relationship between the attainment of first maturity and the body size of this portunid, (4) the composition of the diet of *P. pelagicus* in Leschenault Estuary and whether this is influenced by body size, (5) whether the mesh size of crab pots

influences the size composition of the crabs caught, and (6) the extent to which the commercial catch of *P. pelagicus* in Leschenault Estuary has varied over the years and changes throughout the year, and to elucidate the reasons for the latter changes. Where appropriate, the results of the present study are compared with those previously recorded for *P. pelagicus* in the Leschenault Estuary and also in Cockburn Sound and the Peel-Harvey Estuary, which lie elsewhere in Western Australian waters (Penn 1977; Potter *et al.* 1983), in order to help resolve conflicting conclusions regarding the biology of this portunid in this estuary.

Materials and Methods

Sampling

Portunus pelagicus was collected from sites in both nearshore, shallow (< 1.5 m in depth) and offshore, deeper waters (1.5-2.5 m) in the middle and lower regions of Leschenault Estuary and from nearshore, shallow (< 1.5 m) and offshore, deeper waters (5-7 m) in Koombana Bay (Fig 1). Shallow, nearshore waters were sampled by seine netting, whereas offshore, deeper waters were sampled using crab pots and an otter trawl. Sampling by pots and otter trawls could not be undertaken in the same depths in Koombana Bay as in Leschenault Estuary (*i.e.* 1.5-2.5 m) because in Koombana Bay those water depths coincided with the surf zone. Furthermore, otter trawling was not initiated until it became obvious that even pots with a small mesh size (12 mm) were not catching the small crabs that concurrent sampling for fish had shown to be present in offshore, deeper waters. The months in which sampling by seine netting, crab potting and otter trawling commenced were; Leschenault Inlet - seine nets in April 1996, crab pots in February 1996, otter trawls in June 1997; Koombana Bay - seine nets and crab pots in December 1996, and otter trawls in September 1997. In each case, sampling was carried out monthly until May 1998.

The seine net was 21.5 m long and consisted of two 10 m long wings, each comprising 6 m of 9 mm mesh and 4 m of 3 mm mesh, and a 1.5 m long pocket consisting of 3 mm mesh. The net fished to a maximum depth of 1.5 m and sampled an area of *ca* 116 m². The catches of crabs obtained by seine net are expressed as a density, *i.e.* number of crabs caught per 100 m². On each sampling occasion, seine netting was carried out between 1 000 and 1 500 h at three sites in both the lower and middle regions of Leschenault Estuary and at three sites in Koombana Bay (Fig 1).

All of the 12 crab pots used on each sampling occasion were 630 mm high and 1000 mm in diameter. However, six of the pots were made of 12 mm mesh net, while the other six comprised 76 mm mesh. The 12 mm mesh, which was the strongest of the small meshes that were available, was chosen in an attempt to catch a full-size range of juvenile and adult crabs. The 76 mm mesh was selected as this mesh size is typical of that used by professional fishers in the Leschenault Estuary, Peel-Harvey Estuary and Cockburn Sound, and would thus provide a sample of crabs whose size composition would be similar to that obtained by commercial fishers. All pots were baited with fish. On each sampling occasion, four pots were joined together at
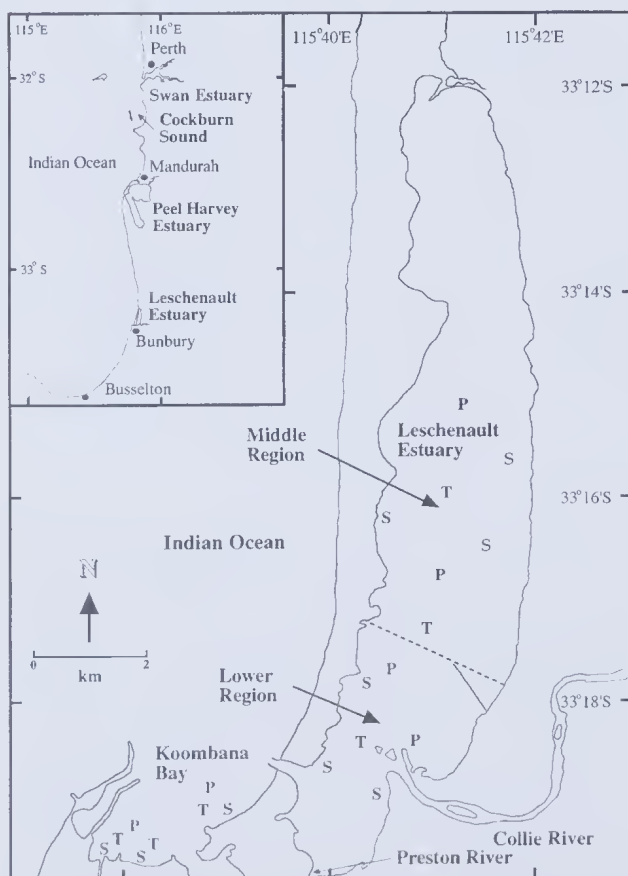

Figure 1. Map showing the sites in Leschenault Estuary and Koombana Bay that were sampled by seine nets (S), crab pots (P) and otter trawls (T). Inset shows location of Leschenault Estuary and Koombana Bay in south-western Australia.

15 m intervals to produce a row of pots, in which the pots with the large mesh alternated with those with the small mesh. The remaining eight pots were then connected in the same manner to create two more rows, in which pots with the large mesh likewise alternated with those with small mesh. On the first night, a row of pots was placed randomly in each of three of the four crab pot sampling sites in Leschenault Estuary and each row was left for 24 h before being retrieved and emptied. On the second night, a row of pots was placed randomly in the fourth site in Leschenault Estuary and in each of the two sites in Koombana Bay. These were also retrieved and emptied after 24 h. The crab pots were linked together in groups of four in a single line so that a single flag could be used to denote their location and thus reduce the chances of that location being spotted by poachers. Catches by pots are expressed as number of crabs caught per pot per day.

The mouth of the otter trawl net was 2.6 m wide, 0.5 m high and 5 m deep. The warp and bridle lengths were 50 and 13 m, respectively. The wings consisted of 51 mm mesh, while the bunt was made of 25 mm mesh. The net was towed by a boat for a distance of ca 50 m at a speed of ca 3-4 km h^{-1}, during which time the trawl covered an area of ca 650 m^2. On each sampling occasion, trawling was carried out between 0800 and 1600 h in each of the three otter trawl sampling sites in both Leschenault Estuary and Koombana Bay. As with the seine net data, the catches of crabs obtained by otter trawl are expressed as a density $i.e.$ number of crabs per 100 m^2.

Prior to sampling, water temperature and salinity were measured near the bottom of the water column at each seine net site in nearshore, shallow waters and at both the top and bottom of the water column at the crab pot and otter trawl sampling sites in offshore, deeper waters. The relative strength of wave (surf) action was also recorded in Koombana Bay.

Measurements

The carapace width (CW) of each crab, $i.e.$ the distance between the tips of the two lateral spines of the carapace, was measured to the nearest 1 mm. The wet weight of each crab was recorded to the nearest 0.1 g.

The fact that the abdomen is far more oval in females than males, when CW is > 30 mm, was used to sex the larger crabs. Since such differences are not well defined in crabs with CW < 30 mm, the pleopods of these smaller crabs (whose characteristics differ between females and males) were dissected out and examined under a dissecting microscope. The sex of these smaller crabs was then distinguished on the basis that the male crab has two pairs of uniramous pleopods whereas the female crab has four pairs of biramous pleopods (Warner 1977). A record was made of whether female crabs were ovigerous (Smith 1982). The fact that for female $P. pelagicus$, the abdomen of the juveniles is triangular whereas that of the adults is almost circular and free of the ventral shell, was used to determine whether or not females had undergone a pubertal moult and had thus either copulated or had not copulated previously (Van Engel 1958; Ingles & Braum 1989). In each month between July 1997 and June 1998, the wet weights of the ovaries of a random sub-sample of crabs from both

Leschenault Estuary and Koombana Bay that had undergone a pubertal moult were weighed to the nearest 0.01 g. The gonad weight of each female crab, that had undergone a pubertal moult, was then expressed as a percentage of its total wet body weight to determine the gonadosomatic index (GSI). The GSI was not determined for ovigerous females, $i.e.$ crabs that had extruded their eggs, and the GSIs have not been provided for male crabs since they were always very low and showed a far less pronounced seasonal trend than that of female crabs.

Since female crabs that have undergone a pubertal moult and thus typically have mated will not commence growing again until after egg extrusion, which can take place within about two weeks (Ingles & Braum 1989), the carapace width at which 50% of crabs undergo a pubertal moult (CW$_{50}$) will also essentially correspond to the CW$_{50}$ at first maturity. The size at which 50% of the female crabs reach maturity (CW$_{50}$) was thus determined from data obtained for a wide size range of female crabs in which each crab had been recorded as either having not undergone or having undergone a pubertal moult, and thus had either not reached the size or had reached the size at which copulation occurs, respectively. A logistic function was fitted to the percentage of those female crabs which, in each 5 mm carapace width interval, had undergone a pubertal moult, using a non-linear technique (Saila $et al.$ 1988), employing a non-linear sub-routine in SPSS (Anon 1988). The logistic equation was PCW = $[1 + e^{(a + bCW)}]$ -1, where PCW is the proportion of crabs that have undergone a pubertal moult at carapace width interval CW, and a and b are constants. The CW$_{50}$ was derived from the equation CW$_{50}$ = - a/b.

Although male crabs do not undergo a morphologically conspicuous pubertal moult, the pattern of growth of their largest chela does change markedly during that moult. This could therefore be used to estimate the size at which male crabs undergo such a moult and have thus attained the size at which they first reach maturity (Reeby $et al.$ 1990; Somerton & Donaldson 1996). Male crabs were thus first separated into three categories, namely (1) juveniles that were small ($i.e.$ CW < 60 mm) and thus below the minimum size at which maturity is usually reached in other populations of $P. pelagicus$, (2) adults that were large, CW > 120 mm, and were thus of a size at which maturity would be expected to have been attained, and (3) juveniles or adults in which the carapace widths lay between 60 and 120 mm. The choice of the above three categories of carapace widths was based on data recorded by Meagher (1971), Ingles & Braum (1989) and Reeby $et al.$ (1990) for the size of juveniles and adults in other populations of $P. pelagicus$. The lengths of the dorsal surface of the propodus of the largest chela of crabs belonging to the first and second of these categories of crabs were then plotted against their carapace widths. Regression lines were fitted by the least sum of squares method to these two data sets, assuming L = a + bCW, where L is the length of the chela propodus, CW is the carapace width and a and b are constants. The two regression lines derived for the relationship between propodus length and carapace width of the (small) juvenile and (large) mature crabs, were then fitted iteratively but with incorporation of the corresponding data for the medium size category (CWs of 60-120 mm), until the two lines which had produced the lowest residual sum of squares were found. The point at which the lines now inter-
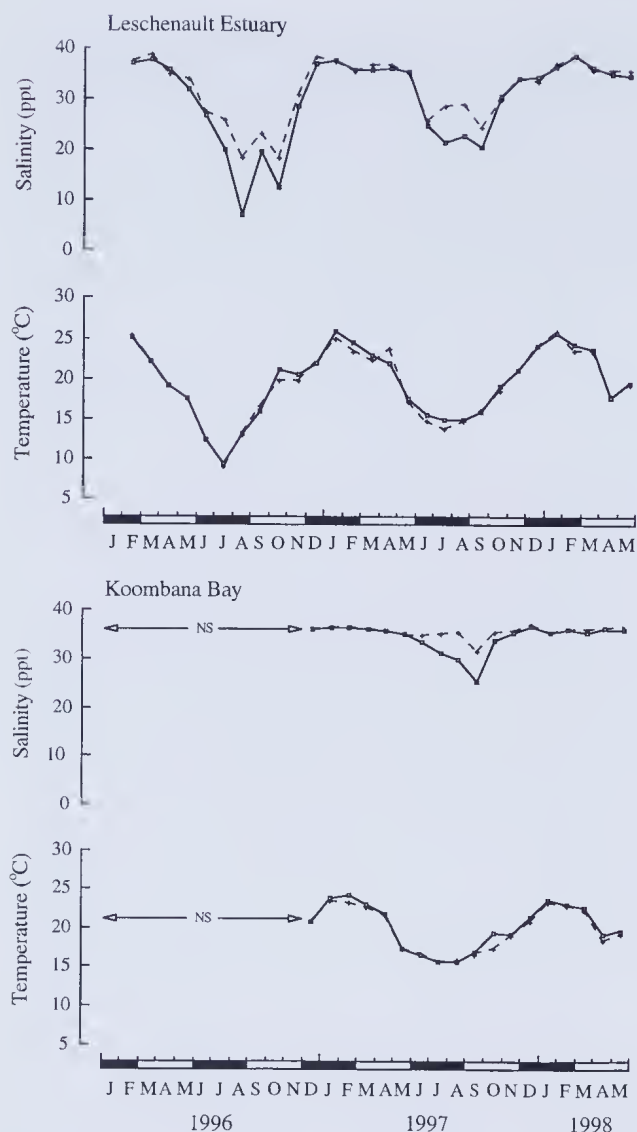
Figure 2. Mean monthly salinities and water temperatures at the bottom and top of the water column in Leschenault Estuary and Koombana Bay. NS, not sampled. ●———— Surface; – – ← – Bottom.

sect was then assumed to provide a good approximation of the carapace width at which there is a pronounced change in the pattern of growth of the largest chela, a feature which is, as mentioned previously, known to be associated in males with the pubertal moult (Reeby *et al.* 1990; Somerton & Donaldson 1996). The next step involved determining whether the point for the relationship between the length of the chela propodus and the carapace width of each crab was closer to the regression line relating these two variables in "juvenile" crabs or in "adult" crabs, as defined above. Each crab was then recorded as either immature or mature, *i.e.* had undergone a pubertal moult. The logistic curve was then fitted to the percentage contributions of mature crabs in each 5 mm carapace width interval.

Diet

Stomachs were removed from sub-samples of 20-30 intermoult (hard shelled) crabs collected by seine netting and otter trawling in each season in Leschenault Estuary.

These crabs were selected so that they covered the entire size range caught on each sampling occasion. The carapace width of each crab was measured. The fullness of the stomach of each crab was recorded, using a scale of 0 (empty) to 10 (full). Each dietary item was identified to the lowest possible taxon under a dissecting microscope and then allocated to one of 13 broader taxonomic categories, which are subsequently referred to as dietary categories. The volumes of each dietary category, and also of ingested sediment, were expressed using the points method (Hynes 1950; Hyslop 1980), which takes into account the overall stomach fullness. Volumetric data provide a good representation of the relative importance of each dietary category, especially in animals such as crabs, which masticate their food and thereby make it difficult to identify the number of individuals belonging to certain prey species (Hyslop 1980). The relative contributions of each dietary category and sediment to the volume in the stomach of each crab (%V) were calculated. The mean contributions of each dietary category to the total volume of the dietary contents were then calculated for crabs with carapace widths ≤ 75 and > 75 mm (CW of 75 mm approximates the mid-point of the size range of *P. pelagicus* in Leschenault Estuary).

Commercial catch

Data on the monthly catches of crabs obtained by commercial fishers using drop nets, and the corresponding data for effort, were extracted from the Fisheries Western Australia Catch and Effort Statistics (CAES). The data covers financial years, *i.e.* July to June, which is appropriate since each year then encompasses the mid spring to autumn period, when crabs are known to be most abundant in estuaries on the lower west coast of Western Australia (*e.g.* Meagher 1971; Potter *et al.* 1983).

Results

Salinity and water temperature

The following account of the trends exhibited by salinity in Leschenault Estuary initially focuses on those occurring at the bottom of the water column in offshore, deeper waters (Fig 2). This is followed by a description of the way in which the salinities at the top of the water column in those waters are modified as a result of the influence of heavy freshwater discharge in winter and how this results in the formation of pronounced haloclines. Attention is drawn to the fact that, in each month, the salinity in shallow, nearshore waters is essentially the same as that recorded at the top of the water column in offshore, deeper waters (Fig 2).

The mean monthly salinities at the bottom of the water column in offshore, deeper waters, *i.e.* 1.5-2.5 m, of Leschenault Estuary in February to April of 1996 were *ca* 35 ppt (Fig 2). They then fell sequentially in subsequent months to a minimum of 18.2 ppt in August, before rising to 23.2 ppt in September and then falling back temporarily to 18.2 ppt in October, due to an overflowing of the Wellington dam on the Collie River and thus to an increase in freshwater discharge into the estuary. They then rose progressively to *ca* 35 ppt in December 1996 and remained close to that level until May 1997, after which they declined to 24-30 ppt in

June to September. Mean monthly salinities then rose progressively to 35 ppt in December 1997 and remained at or just above this level through to May 1998 (Fig 2).

Mean monthly salinities at the surface of the water column in offshore, deeper waters of the estuary followed the same seasonal trends as those exhibited by bottom salinities (Fig 2). However, salinities at the surface declined to appreciably lower levels than those at the bottom of the water column in July to October of 1996 and in July to September of 1997. This reflects the fact that a substantial amount of the increase that occurs in the input of freshwater discharge from the Collie and Preston rivers into Leschenault Estuary in winter, following the onset of seasonal rains, flows out at the surface of the estuary and thereby produces a conspicuous halocline in those months. The maximum difference between surface and bottom salinities was the 11.1 ppt recorded in August 1996 (Fig 2).

Mean monthly water temperatures at the bottom of the water column in offshore, deeper waters of Leschenault Estuary declined sequentially from 25.4 °C in February 1996 to a minimum of 8.9 °C in July and then rose to 25.0 °C in January 1997 (Fig 2). They subsequently declined gradually to 23.7 °C in April and then more rapidly to ca 14.5 °C in July, before rising progressively over the ensuing six months to reach a peak of 26.1 °C in January 1998 and then declining to between 17.9 and 19.3 °C in April and May. In each month, the mean water temperatures at the surface of the water column in offshore, deeper waters of Leschenault Estuary were the same or similar to those at the bottom of the water column (Fig 2). Thus, a marked thermocline was never formed in the estuary. In each month, the mean water temperature in nearshore, shallow waters was always very similar to that recorded at the surface in offshore, deeper waters.

In Koombana Bay, the mean monthly salinities at the bottom of the water column remained at ca 35ppt in each month between December 1996 and May 1998, except in September 1997 when they declined to 31.6 ppt (Fig 2). Mean monthly salinities in the surface of the offshore, deeper waters of Koombana Bay remained at ca 35 ppt between December 1996 and May 1997, before declining sequentially to a minimum of 25.4 ppt in September, which was appreciably lower than the mean salinity at the bottom of the water column in that month. This decline in salinity was due to a continuous heavy discharge of fresh water from the Collie and Preston rivers into the lower end of Leschenault Estuary and then out through the channel into Koombana Bay. This very substantial input of freshwater into Koombana Bay accounts for the development of a pronounced halocline in this embayment in July to September 1997 (Fig 2).

Mean monthly temperatures at the bottom of the water column in offshore, deeper waters of Koombana Bay declined from 23.4 °C in January 1997 to a minimum of ca 16 °C in July and August 1997, before rising to 17.3 °C in October and then to a peak of 23.1 °C in January 1998 (Fig 2). In virtually all months, the mean temperature at the surface of offshore, deeper waters was usually the same or very similar to that at the bottom of the water column. However, a slight thermocline was recorded in October 1997, when the mean surface water temperature was 2 °C

higher than that at the bottom of the water column (Fig 2).

As was the case in Leschenault Estuary, the mean salinity and water temperature in nearshore, shallows of Koombana Bay in any month were very similar to those at the top of the water column in offshore, deeper waters in the same month.

Monthly density and catch rates

In each month, the densities of blue swimmer crabs at the three sites in nearshore, shallow waters of the middle region of Leschenault Estuary were almost invariably not significantly different from those at the three sites in corresponding waters of the lower region of this estuary. Thus,
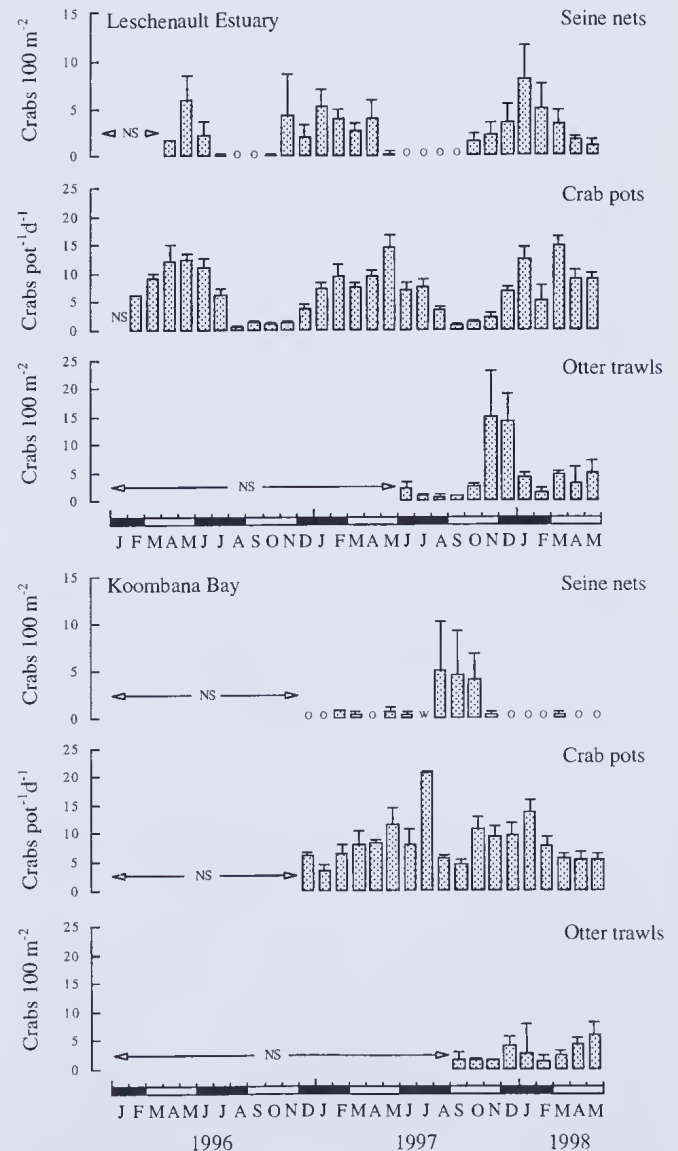

Figure 3. Mean +1 se for densities or catch rates of *Portunus pelagicus* in Leschenault Estuary and Koombana Bay, based on data derived from samples collected by seine nets in nearshore, shallow waters and by crab pots and otter trawls in offshore, deeper waters. The black rectangles on the X axis refer to summer and winter months and the open rectangles to autumn and spring months. NS, not sampled; W, wave action too strong for sampling; 0, zero catch.

the densities of crabs at each of those six seine net sampling sites in each month have been pooled. The mean monthly density of crabs in the six nearshore, shallow sites of the Leschenault Estuary declined from 5.8 crabs 100 m^{-2} in May 1996 to 0 in August and September, before rising to 4.3 crabs 100 m^{-2} in November and remaining at between 2.0 and 5.3 crabs 100 m^{-2} until May 1997, when it declined to 0.3 crabs 100 m^{-2} (Fig 3). No crabs were caught at any of the six seine net sampling sites in the estuary between June and September 1997. However, crabs were caught again at these sites in October, the catches in that month corresponding to a mean density of 1.4 crabs 100 m^{-2}. Mean monthly densities increased to 2.3 crabs 100 m^{-2} in November and then to a maximum of 7.9 crabs 100 m^{-2} in January 1998, after which they declined progressively to 1.0 crab 100 m^{-2} in May (Fig 3).

The size distributions of female crabs caught in pots with 12 mm mesh during 1996 were essentially the same as those in pots with 76 mm mesh, and this was also the case with male crabs (Fig 4). However, in the case of the catches obtained in both the 12 and 76 mm mesh pots, the proportions of crabs with a CW > 130 mm were greater for females than males, whereas the reverse pertained with crabs with a CW < 120 mm. This point is reflected by differences in the mean values for the carapace widths. Thus, the mean carapace width of female crabs caught in 12 and 76 mm mesh pots *i.e.* 124.2 and 124.9 mm respectively, were each significantly greater (P < 0.05) than those of male crabs caught in pots with corresponding meshes, *i.e.* 119.4 and 118.9 mm respectively. Since there was no significant difference between the mean carapace width of female crabs caught in pots with 12 and 76 mm meshes and the same

was also true for male crabs, the catches of each sex in pots with both mesh sizes have been pooled (Fig 3).

The mean monthly catch of crabs pot^{-1} d^{-1} in offshore, deeper waters of Leschenault Estuary in 1996 rose from 6.2 in February to 12.5 in May, and then fell after July to < 1.3 between August and November (Fig 3). Catch rates, using the same units, began to rise in December and subsequently peaked at 14.5 in May 1997, before declining to their minima of 0.8 in September, one month later than in the previous year. Mean catch rates subsequently remained below 2.0 crabs pot^{-1} d^{-1} in October and November, but then remained at between 5.2 and 14.9 crabs pot^{-1} d^{-1} between December 1997 and May 1998 (Fig 3).

The mean monthly densities of crabs in offshore, deeper waters, based on data obtained from otter trawl samples collected in similar regions of the Leschenault Estuary as those in which the traps were laid, declined from 2.1 crabs 100 m^{-2} in June 1997 to less than 0.6 crabs 100 m^{-2} in August and remained below 0.9 crabs 100 m^{-2} in September, before rising sharply to *ca* 15 crabs 100 m^{-2} in both November and December (Fig 3). Mean monthly densities in January to May 1998 lay between 1.5 and 5 crabs 100 m^{-2}.

The mean monthly densities of crabs in the shallows of Koombana Bay, based on data derived from samples collected by seine netting in the three widely-distributed nearshore, shallow sites in this embayment, were either zero or less than 0.8 crabs 100 m^{-2} in all months except August, September and October 1997, when they lay between 4.0 and 5.1 crabs 100 m^{-2} (Fig 3).

The mean monthly catch rate of crabs by pots in offshore, deeper waters of Koombana Bay showed no consistent
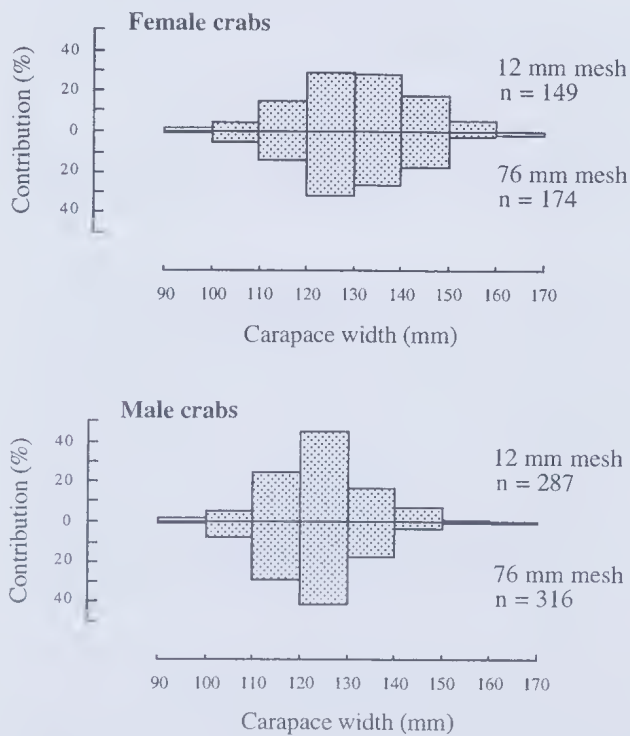

Figure 4. Carapace-width histograms for female and male *Portunus pelagicus* caught by crab pots with 12 and 76 mm meshes between February 1996 and January 1997. n is the number of crabs measured.
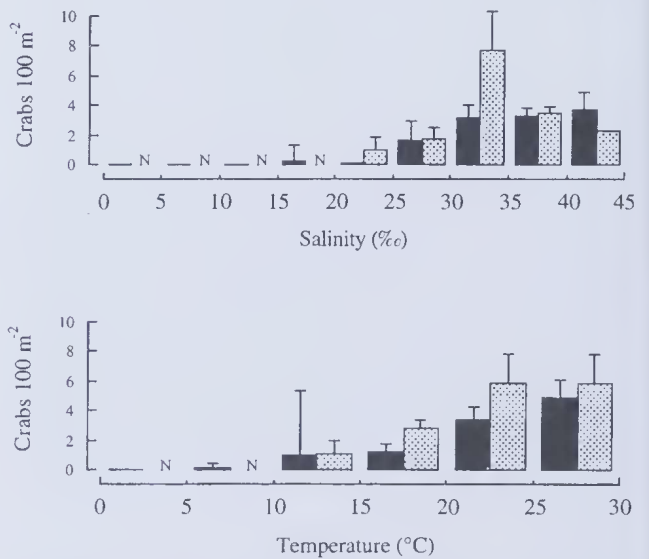

Figure 5. Mean +1 se for densities of *Portunus pelagicus* in different salinity and water temperature intervals in nearshore, shallow and offshore, deeper waters of the Leschenault Estuary, based on data collected using seine nets between April 1996 and May 1998 and otter trawls between June 1997 and May 1998, respectively. Values for salinities and temperatures at the bottom of the water column were used in the case of deeper waters. N indicates that salinities and temperatures were not recorded in deeper, offshore waters during sampling by otter trawl. ■ Nearshore, shallow waters; ▨ Offshore, deeper waters.

seasonal trends during the study (Fig 3). The overall mean catch rate throughout the sampling period was 8.3 crabs pot^{-1} d^{-1}, with the highest mean monthly catch rate in this period being the 20.7 crabs pot^{-1} d^{-1} recorded in July 1997 (Fig 3). Otter trawling in Koombana Bay between September 1997 and May 1998 yielded catches that corresponded to mean monthly densities of 1.3 to 5.1 crabs 100 m^{-2} (Fig 3).

The mean densities of *P. pelagicus* in nearshore, shallow waters of Leschenault Estuary, based on samples collected by seine net, were similar in each of the three 5 ppt salinity intervals between 30 and 45 ppt, with values for these intervals ranging only from 3.2 to 3.7 crabs 100 m^{-2} (Fig 5). Few crabs were caught in the shallows when salinities were < 20 ppt. The mean densities of crabs in offshore and slightly deeper waters, based on samples collected by otter trawl, lay between 1.1 and 7.7 crabs 100 m^{-2} in each 5 ppt salinity interval between 20 and 45 ppt and were greatest in salinities of 30.0-34.9 ppt and least in salinities of 20.0-24.9 ppt.

The mean densities of crabs in nearshore, shallow waters of Leschenault Estuary ranged downwards from 4.9 crabs 100 m^{-2} in water temperatures of 25-29.9 °C to 3.4 crabs 100 m^{-2} in 20.0-24.9 °C and 1.0 crabs 100 m^{-2} in 10.0-14.9 °C (Fig 5). A similar trend was observed in offshore, deeper waters, where the mean densities declined from *ca* 5.9 crabs 100 m^{-2} in 20.0-29.9 °C to 1.1 crabs 100 m^{-2} in 10.0-14.9 °C. Virtually no crabs were caught in the estuary when water temperatures fell below 10 °C.

Size and growth

Since the carapace width of crabs caught in Leschenault Estuary by pots with both 12 and 76 mm mesh were > 90 mm in the 12 months between February 1996 and January 1997 (Fig 4), and yet many crabs were present in the estuary below this size at certain times of the year, there was a high level of selectivity for large crabs using pots. The size data for crabs in pots have thus not been included in the monthly size-frequency histograms shown in Figs 6 and 7. Since the monthly trends exhibited by the size-frequency data for *P. pelagicus* in seine net samples collected in Leschenault Estuary were the same in each year and the same was true for Koombana Bay, the carapace width data given in Figs 6 and 7 for crabs in both water bodies have utilised pooled size data obtained from seine netting in each of the corresponding months of the different years.

Samples of female crabs collected in Leschenault Estuary in June contained a small group of small crabs with carapace widths between 30 and 90 mm and a small group of larger crabs with carapace widths between 100 and 160 mm (Fig 6). In July to September, the cohort of larger crabs was no longer present and the smaller crabs were present in only very low numbers. The cohort, which corresponded to the smaller crabs caught in June, started to increase in numbers in October and was still well represented in May, by which time its size range corresponded to that of the small group of larger crabs caught in June. The modal carapace width class of this cohort had increased from 60-69 mm in November to 70-79 mm in December and 90-99 mm in January to 100-109 mm in March and 110-119 mm in May (Fig 6). Small numbers of a new cohort of small crabs, with carapace widths of 30 to 79 mm, were present in Feb-

ruary to May. These corresponded to the cohort of small crabs found in June. The trends exhibited by the monthly carapace-width frequency histograms for male crabs were essentially the same as those just described for female crabs (Fig 6).

The above trends demonstrate that small crabs, representing the 0+ age class, are recruited into Leschenault Estuary in small numbers in late summer and autumn. The numbers of this cohort in the estuary then decline in winter and early spring, before starting to rise markedly in mid to late spring as the water temperatures start increasing markedly. This cohort was represented by large numbers in December to February, in which months its members were, on the basis of a late spring/summer spawning period (see later), now *ca* 1 year old. The corresponding cohort, now representing 1+ crabs, was relatively abundant until late autumn, but then declined in numbers in June and had essentially disappeared from the estuary in the ensuing winter and early spring months.

The size distributions of both female and male crabs caught collectively by seine net and otter trawl in Koombana Bay were similar in each month between August and December, with the vast majority of both sexes having a CW > 80 mm (Fig 7). The carapace widths of the corresponding cohort increased slightly in the ensuing months, and more particularly in the case of male crabs. The new 0+ cohort, represented by crabs with carapace widths of 20 to *ca* 90 mm, first appeared in low numbers in February and in more substantial numbers in April and May (Fig 7).

The carapace widths of all female and male crabs caught by crab pots in each month of the year in the Leschenault Estuary and Koombana Bay were almost invariably > 90 mm (Fig 8). Indeed, the modal carapace width was usually between 100 and 130 mm. The virtual absence in pots of crabs with a CW < 90 mm may reflect avoidance of the bait in pots by smaller crabs as a result of the more aggressive behaviour of large crabs (Warner 1977) and/or a greater preference of larger crabs for fish (see later), which was used as bait. The modal carapace widths did not thus show a progression of the type that was exhibited by crabs caught in Leschenault Estuary using seine nets and otter trawls (*cf* Figs 6, 8). It is also noteworthy that, while all of the crabs caught in seine nets and otter trawls between the middle of winter and early spring had a carapace width < 120 mm (Fig 6), a few crabs with carapace widths > 120 mm were caught in pots during this period (Fig 8). This indicates that a few 1+ crabs remain in the estuary during this period.

Sex ratio

The overall sex ratios of crabs that had a CW < 90 mm and were caught by otter trawl in Leschenault Estuary and Koombana Bay in the different months were often close to parity, particularly in Leschenault Estuary (Fig 9). A Chi-squared test showed that there was no significant overall deviation from a 1:1 ratio of females to males in either locality. However, amongst crabs with a CW > 90 mm in the samples collected by otter trawl, the ratio of females to males was significantly less than parity in Leschenault Estuary (1:1.8), whereas the reverse was true for Koombana Bay
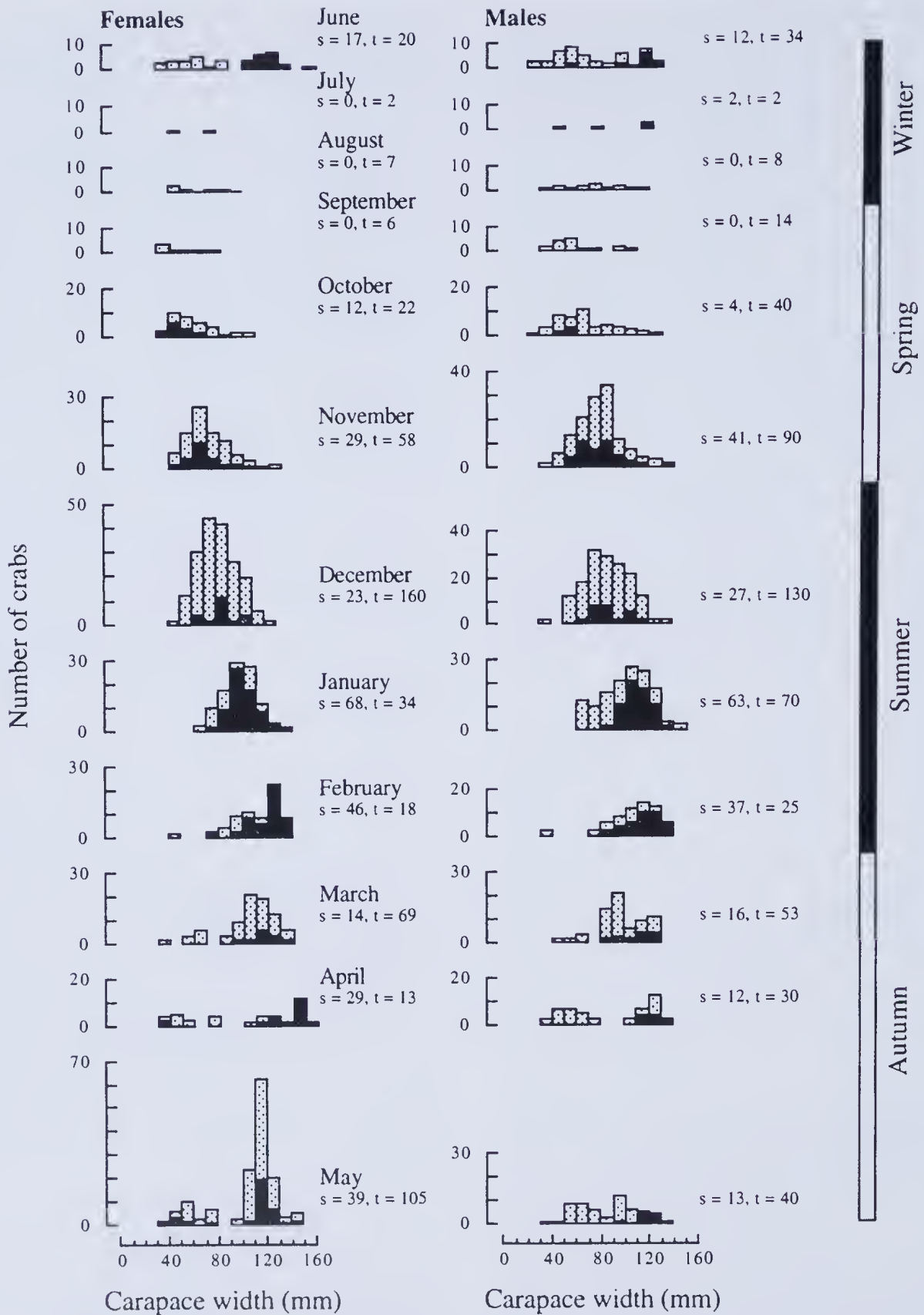
Figure 6. Monthly frequency histograms for the carapace widths of female and male *Portunus pelagicus* in Leschenault Estuary, based on data derived from samples collected by seine net in nearshore, shallow waters between April 1996 and May 1998 and by otter trawl in offshore, deeper waters between June 1997 and May 1998. The data obtained by both methods in each month have been adjusted to correspond to a total area sampled of 2000 m^{-2}, which is similar to the area covered during the three otter trawls carried out monthly in any one year and by seine netting in the corresponding months over three years. Number of crabs caught by seines and trawls are denoted by s and t, respectively.
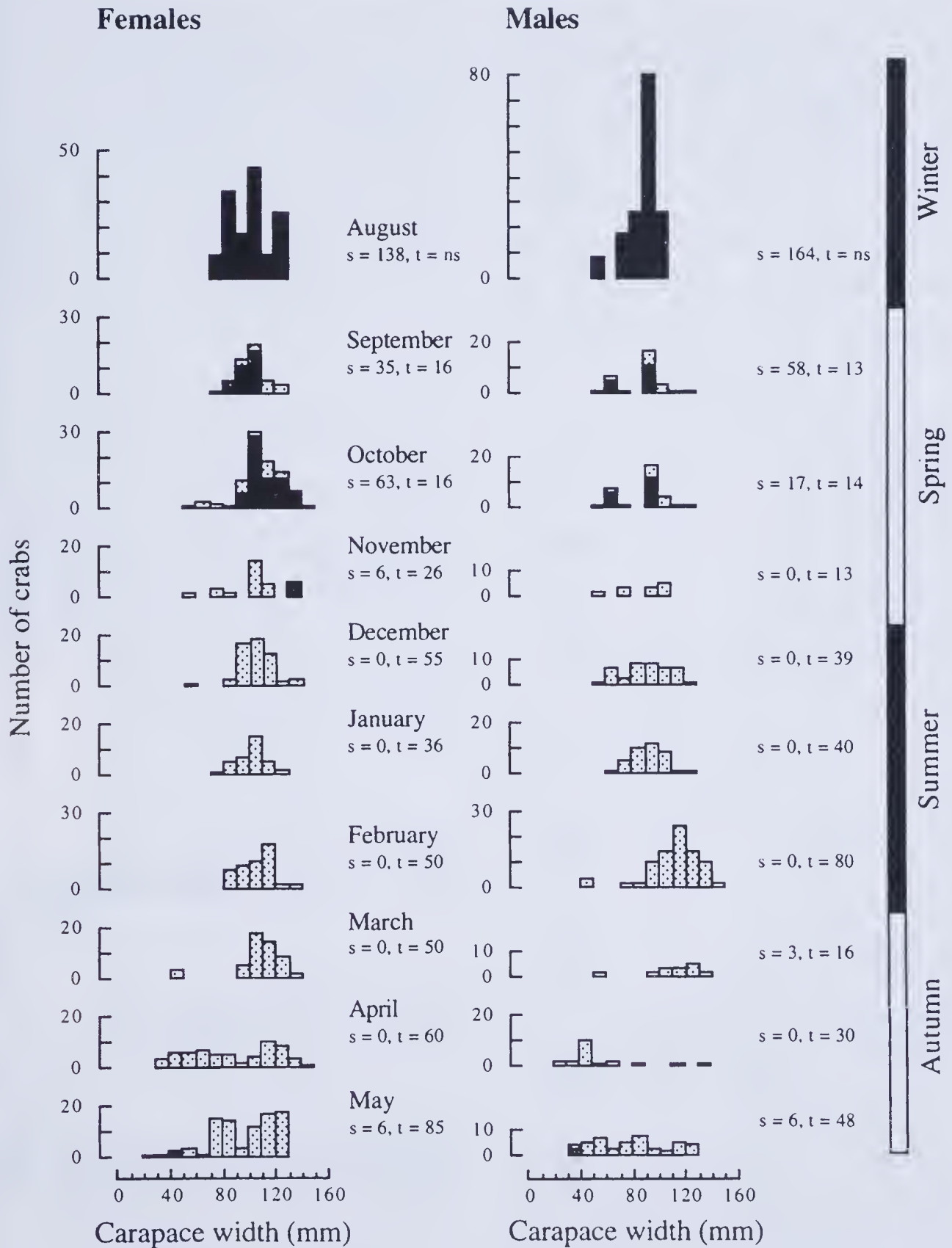
Figure 7. Monthly frequency histograms for the carapace widths of female and male *Portunus pelagicus* in Koombana Bay, using data derived from samples collected by seine nets in nearshore, shallow waters between December 1996 and March 1997 and by otter trawls in offshore, deeper waters between September 1997 and March 1998. The data obtained by both methods in each month have been adjusted to correspond to a total area sampled of 2000 m^{-2}, which is similar to the area covered during the three otter trawls carried out monthly in any one year and by seine netting in the corresponding months over three years. Number of crabs caught by seines and trawls are denoted by s and t, respectively.

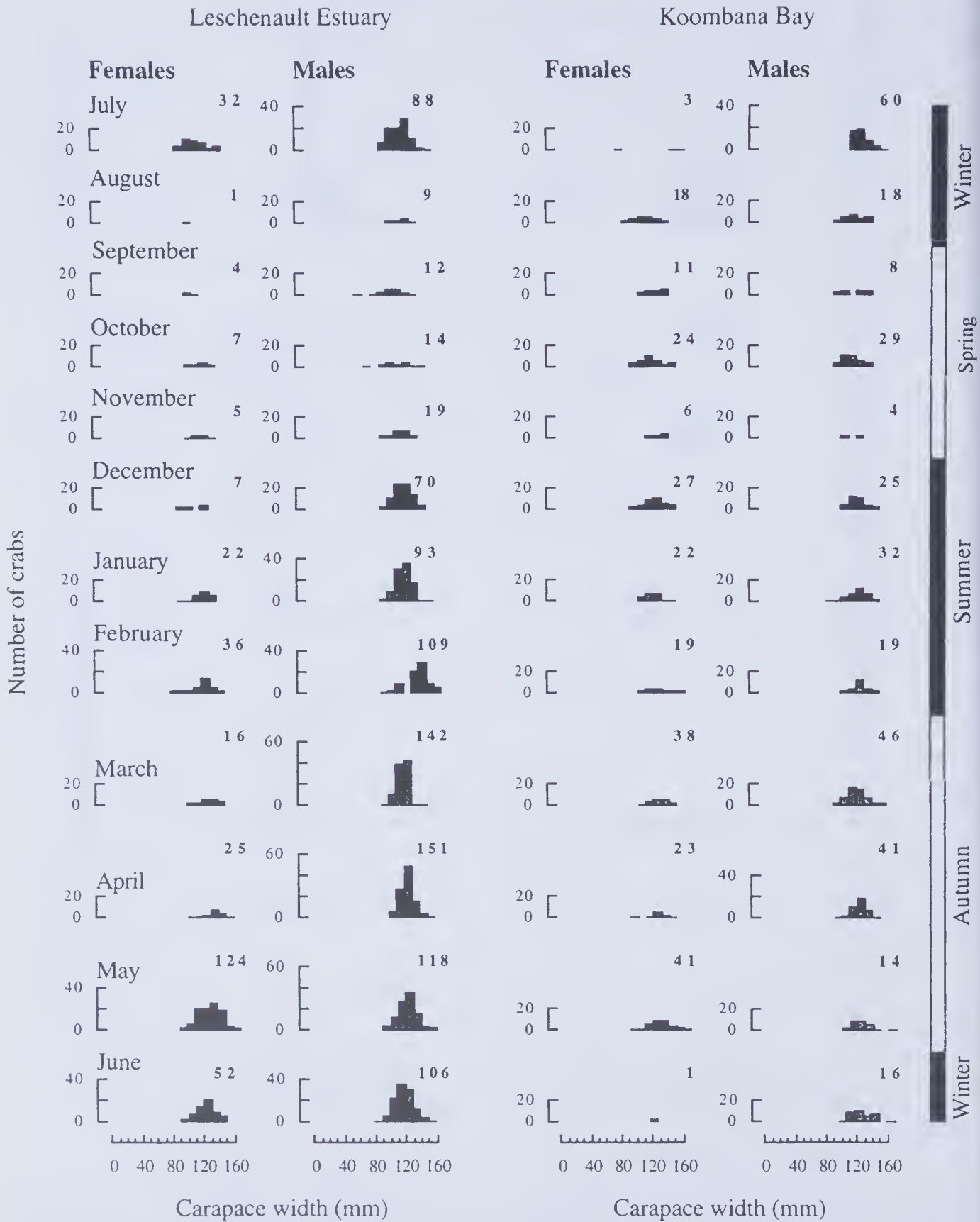Leschenault Estuary

Koombana Bay

Figure 8. Monthly frequency histograms for the carapace widths of *Portunus pelagicus* caught in crab pots in Leschenault Estuary between February 1996 and May 1998 and in Koombana Bay between 1996 and May 1997. Data for the corresponding months of the year have been adjusted so that they correspond to a monthly mean. Sample size is given for each monthly catch of female and male crabs.

(1:0.5). Although the ratio of females to males in pot catches was likewise greater in Leschenault Estuary, this difference was even more pronounced, with the overall sex ratio of females to males being 1:3.8. The sex ratio also differed significantly from parity in the case of crab pot catches obtained from Koombana Bay, but in this case the difference between the contributions of the two sexes was not as extreme, with the overall ratio of females to males being 1 to 1.7. However, in both Leschenault Estuary and Koombana Bay, the proportion of female crabs was less in the samples obtained by crab pots than in those that were caught by otter trawls and likewise had a CW > 90 mm. This implies that crab pots have a greater tendency to catch male than female crabs, which may be related to the greater levels of activity exhibited by male crabs (Sumpton & Smith 1990).

Reproductive biology

The smallest female *P. pelagicus* that had undergone a pubertal moult in Leschenault Estuary and Koombana Bay and could thus be characterised as having attained the size at which maturity occurs, had a carapace width of 94 mm. Maturity was attained by *ca* 75% of female crabs with carapace widths of 100-105 mm and by all of those with carapace widths of 125-130 mm (Fig 10). The logistic curve fitted to the data for the percentage numbers of female crabs that had undergone a pubertal moult in sequential 5 mm carapace width intervals yielded a value of 97 mm for the carapace width at which 50% of female crabs first become mature (Fig 10). The corresponding CW_{50} for male crabs was 84 mm (Fig 10).

The mean monthly GSIs of female crabs in Koombana Bay in 1997, utilising data for individuals that had under-

gone a pubertal moult, rose progressively from 1.2 in July to a maximum of 4.6 in October, before declining to 1.7 in December (Fig 11). They subsequently fell to their minima of *ca* 0.2 in February and March of 1998, but then increased to 1.5 in May, a value similar to that recorded in July 1997. Although the trends exhibited by the mean monthly GSIs of female crabs were similar in Leschenault Estuary to those exhibited in Koombana Bay, the maximum values were far lower, *i.e.* 1.9 *vs* 4.6 (Fig 11).

Between July 1997 and May 1998, ovigerous females were found in Koombana Bay in each month between October and January and in May and in the Leschenault Estuary in each month between November and May except for February and April (Fig 11). However, the majority of ovigerous females was caught in November to January in Koombana
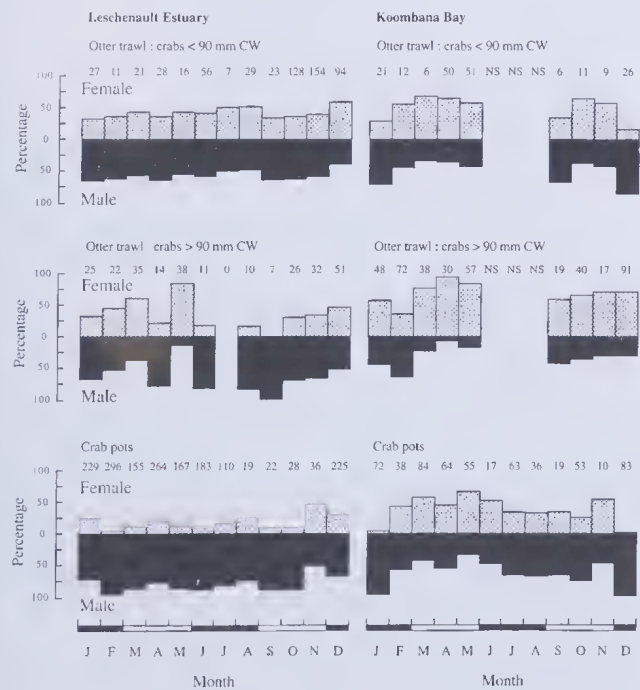

Figure 10. Top: Percentage of those females in each sequential 5 mm carapace width interval which had not undergone a pubertal moult and would thus not have mated and for those which had undergone a pubertal moult and were therefore of mature size. The logistic curve was fitted to the percentage of crabs that had undergone a pubertal moult in order to determine the CW_{50} at first maturity. **Bottom:** For males, the logistic curve was fitted to the carapace widths of those crabs which, from the relationships between the lengths of the propodus of the largest chela and the carapace widths, were capable of mating and were thus adults of mature size (see text for full details of methodology). Arrows denote CW_{50} for size at maturity of female and male crabs.

Figure 9. Percentage number of female and male *Portunus pelagicus* in samples collected by otter trawls and crab pots, respectively. Monthly sample sizes are given above each histogram. The black rectangles on the x axis refer to summer and winter months and the open rectangles to autumn and spring months.
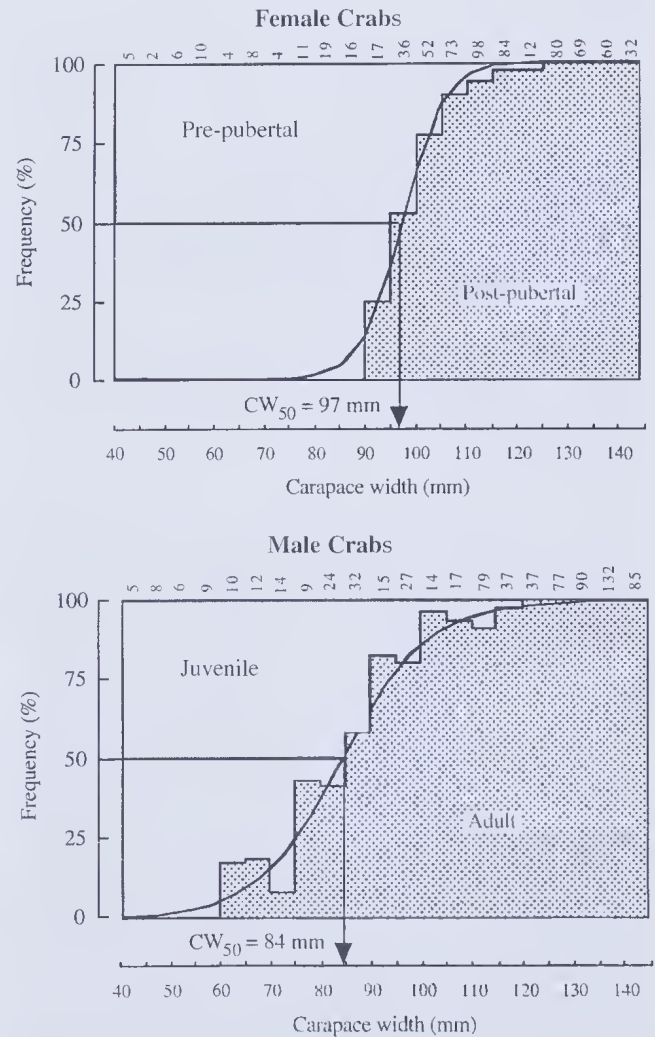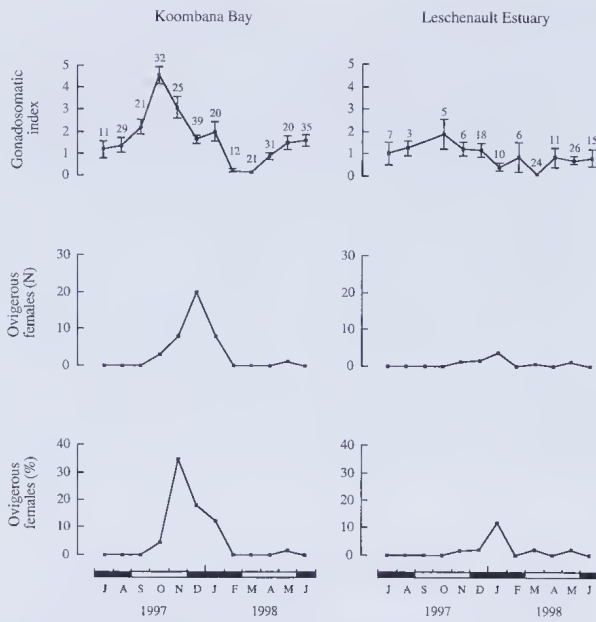
Koombana Bay   Leschenault Estuary

Figure 11. Monthly values for the mean gonadosomatic index ±1 se of female crabs, which had undergone a pubertal moult, the number of ovigerous female crabs and the prevalence (%) of ovigerous crabs amongst female crabs with a CW > 97 mm, the CW_{50} at which female crabs first reach maturity. The numbers and prevalence of ovigerous crabs caught monthly in Koombana Bay have been adjusted so that they are based on the same effort as that employed monthly in Koombana Bay, *i.e.* the use of three seines, three otter trawls and eight crab pots in each month. The black rectangles on the x axis refer to summer and winter months and the open rectangles to autumn and spring months.

Bay and in December and January in Leschenault Estuary. Furthermore, both the numbers and prevalence of ovigerous crabs were far greater in Koombana Bay than in Leschenault Estuary (Fig 11). This point is emphasised by the fact that the maximum monthly values for the number and prevalence of ovigerous crabs were 20.0 and 34.8% in Koombana Bay, respectively, and 4.9 and 11.9% in Leschenault Estuary, respectively. The above trends exhibited by the prevalence of ovigerous crabs parallels those recorded in the previous year, based on data derived from samples that were collected using just seine nets and crab pots (data not shown). The above data on ovigerous females provide overwhelming evidence that spawning occurs in Koombana Bay and that it takes place predominantly between the middle of spring and middle of summer.

Diet

Based on pooled samples for all size classes of intermoult *i.e.* hard shelled crabs, the assemblage of *P. pelagicus* in Leschenault Estuary feeds largely on a wide range of benthic invertebrates, such as amphipods, polychaetes, bivalve molluscs, and also on teleosts *e.g.* gobiids. However, the diets of small crabs (CW ≤ 75 mm) and large crabs (CW > 75 mm) differ. Thus, for example, the volumetric contribution made to the diet by amphipods declined markedly from 41.6% in small crabs to 13.3% in large crabs, whereas those of polychaetes and teleosts rose from 13.1 and 2.2% to 27.0 and 10.3%, respectively (Fig 12).
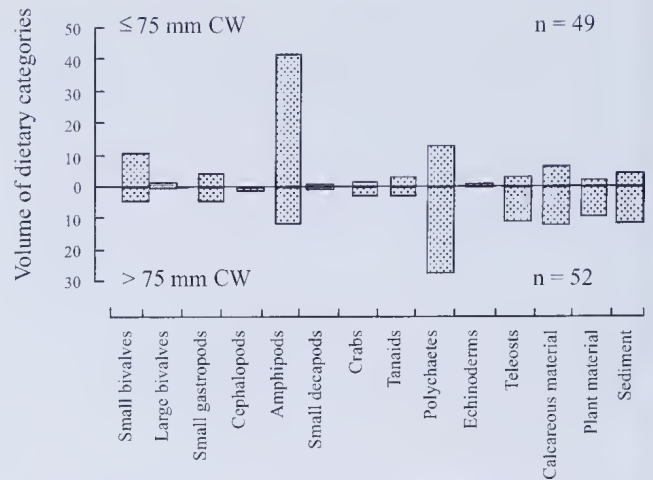

Figure 12. Frequency histograms showing the percentage contributions of the volume of different dietary categories to the total volume of the diets of two size categories (CW ≤ 75 and > 75 mm) of *Portunus pelagicus* collected in Leschenault Estuary. n is the number of samples.

Commercial fishery

The annual commercial catches of blue swimmer crabs in Leschenault Estuary between 1983/84 and 1995/96 ranged from a low of 1 027 kg in 1993/94 to a high of 7 700 kg in 1983/84 (Fig 13), with an annual mean of 4 382 ± 566.9 (se) kg. The annual commercial fishing effort for blue swimmer crabs, as measured by the total number of days spent fishing by commercial fishers for this portunid each year, remained above 130 days year[-1] from 1983/84 to 1992/93, except in 1988/89, but then declined to < 108 days year[-1] from 1993/94 to 1995/96 (Fig 13). The maximum number of days spent fishing in any one year was the 228 days in 1989/90. In contrast to effort, the highest catch per unit efforts (CPUEs), as reflected by kg wet weight of crabs caught per days fished, were recorded in 1994/95 and 1995/96. The minimum and maximum annual values for CPUE *i.e.* 61.0 and 312.1 kg wet weight per days fished, were recorded in 1988/89 and 1994/95 respectively.

The mean monthly commercial catches of blue swimmer crabs in Leschenault Estuary changed markedly throughout the year (Fig 14). Thus, they were very low in July to November *i.e.* < 122 kg, but then rose markedly to 532 kg in December and 1 211 kg in January, before subsequently falling sequentially to 484 kg in April, 214 kg in May and 52 kg in June. The mean monthly values for effort followed the same pattern as that exhibited by catch (Fig 14). Thus, the total number of days spent fishing for crabs remained less than four in each month between July and November, before rising to maxima of 31 in January and 26 in February, and then declining sequentially in each ensuing month to only two days in June. Although the monthly trends exhibited by CPUE were very similar to those displayed by catch and effort, the CPUE started to rise slightly earlier *i.e.* September to November, and reached a maximum one month later *i.e.* February (Fig 14).

A creel census (*per. com.* N. Sumner *et al* Fisheries WA 2000) conducted by Fisheries Western Australia demonstrates that there is a considerable recreational fishery for *P. pelagicus* in Leschenault Estuary.
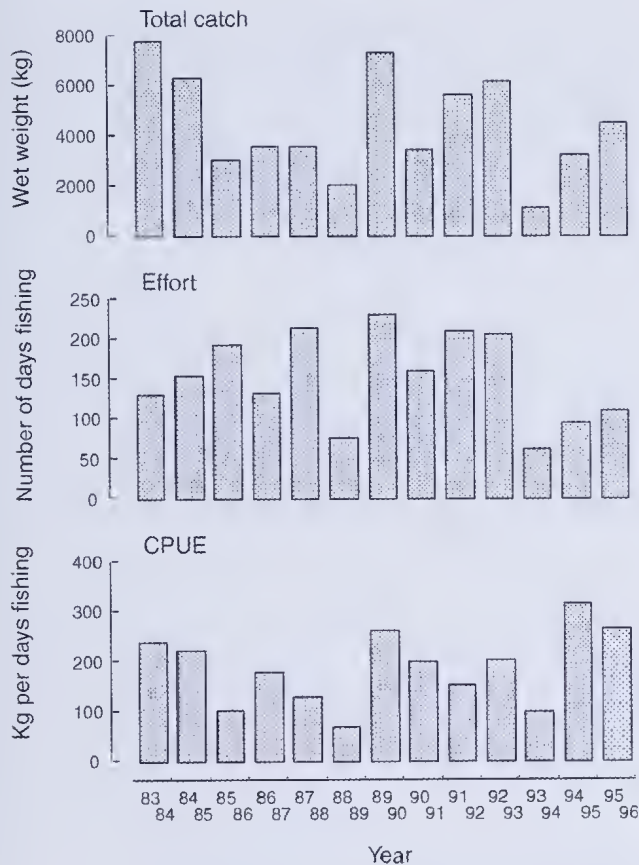
Figure 13. Annual values for total catch, effort and catch per unit effort (CPUE) for the commercial fishery for *Portunus pelagicus* in Leschenault Estuary between 1983/84 and 1995/96. Each "year" runs from 1 July to 30 June.
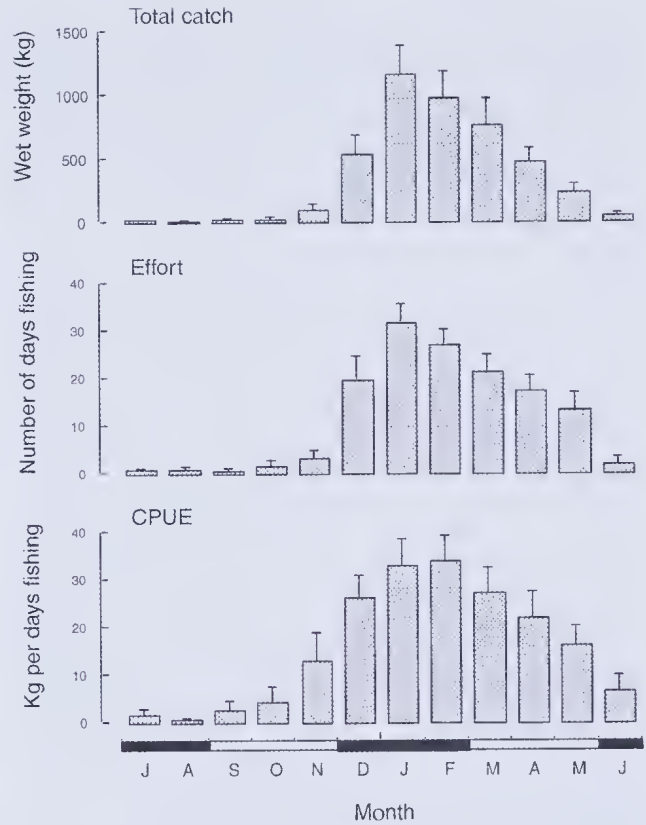

Figure 14. Mean monthly values +1 se for total catch, effort and catch per unit effort (CPUE) for the commercial fishery for *Portunus pelagicus* in Leschenault Estuary between 1983/84 and 1995/96. The black rectangles on the x axis refer to summer and winter months and the open rectangles to autumn and spring months.

Discussion

Seasonal trends

The mean monthly densities of *Portunus pelagicus* in nearshore, shallow waters of Leschenault Estuary, based on data derived from seine net sampling, were highest between mid-spring and mid-autumn and declined to very low or zero levels during winter and early spring. Although the catch rates derived from data using pots in offshore, deeper waters followed similar seasonal trends, they tended to start rising markedly a little later, *i.e.* early summer *vs* early to mid spring, and to remain at a relatively high level for longer, *i.e.* until mid winter *vs* mid- to late autumn. The tendency for the catches in pots to start increasing later can be attributed to the fact that it is not until early summer that the carapace widths of a substantial number of crabs in the estuary start to exceed 90 mm, the minimum size at which crabs are usually caught by crab pots. The maintenance of relatively high catches in pots in offshore, deeper waters for a longer period than in nearshore, shallow waters may reflect in part a tendency for crabs in autumn to move from the shallows, as salinities begin to decline markedly in those waters, out into deeper waters below the halocline where salinities remain higher. It may also be related to the characteristics of the regime we used to sample with crab pots. For example, it is likely that pots soon become "saturated" in summer, when crabs are abundant, but because they were always laid for a long period

(24 hours), they were still able to approach or even reach "saturation" in mid-winter, even though fewer crabs remained in the estuary at this time. The view that increases in the number of crabs in a pot during summer would increasingly reduce the likelihood of further crabs entering that pot, and thus lead relatively soon to saturation, is consistent with the results of studies on other portunid species (see Williams & Hill 1982).

The conclusion that the tendency for the catches of crabs by pots to remain high well into winter may not reflect precisely the trends exhibited by the relative abundance of crabs in the estuary is supported by the fact that they do not parallel precisely those displayed by the mean monthly values for the CPUE for the commercial fishery, a fishery which is based on using drop nets for 25-30 minutes on eight or nine occasions during the day. Thus, in contrast to the trends exhibited by crab pot catches, the CPUE for the commercial fishery declined progressively after January and February, with the result that by June it was less than 20% of the values in those two earlier months. Yet, the possibility cannot be excluded that this decline in CPUE also partly reflects the influence of declining temperatures on the activity of crabs and thus their catchability by "passive" fishing methods such as drop netting (Hill 1980; Williams & Hill 1982). Since water temperatures are particularly low between the middle of winter and early spring, such an effect could be invoked to account in part for the particularly low catches recorded in crab pots during that period. However, it is relevant that

the catches of crabs obtained by the active fishing methods of seine netting and otter trawling, which, unlike those collected in pots also include small crabs, likewise fell to very low levels in winter and early spring, but then rose sharply during late spring as salinities and water temperatures started to rise markedly. There can thus be little doubt that crab numbers in the estuary undergo a real and pronounced decline in winter, when salinities and water temperatures decline to their lowest levels.

From our data, it is evident that juvenile *P. pelagicus* start to enter Leschenault Estuary in substantial numbers during spring and that, while their abundance peaks in summer, substantial numbers of crabs are still found in this estuary until early autumn. Since the marked decline in crab numbers that subsequently occurs in the estuary during winter and early spring is accompanied by a conspicuous rise in the densities of crabs in the shallows of Koombana Bay at these times, it is assumed that at least some of the crabs which emigrate from the estuary in winter, move into nearshore, shallow waters of the above embayment. However, although the largest catch taken by pots in offshore deeper waters of Koombana Bay was recorded in winter, there was no marked tendency for the catch rates by pots in that environment to show any conspicuous seasonal trend. Thus, a substantial number of larger crabs, *i.e.* those of a size that are caught in pots, are present in offshore, deeper waters of Koombana Bay throughout the year. In this respect, our data support the conclusions of Anon (1983), rather than those of Meagher (1971) who considered that virtually all of those crabs that are in Koombana Bay at the end of winter subsequently migrate into the estuary in spring.

Our data, and also those for the Peel-Harvey Estuary (Potter *et al.* 1983), demonstrate that the densities of *P. pelagicus* are greatest in estuaries when salinities and water temperatures are high and that they are very low when these variables decline below 25 ppt and 10 °C, respectively. However, since the trends exhibited by salinities and water temperatures are highly correlated, it is dangerous to use techniques, such as stepwise multiple regressions, to attempt to disentangle which of these variables has the greatest influence on the movements of crabs into and out of the Leschenault Estuary. However, a comparison of the situation in Leschenault Estuary with that in the Peel-Harvey Estuary indicates that salinity exerts a profound influence on whether or not crabs remain within the estuary. For example, it is relevant that, although the overall trends exhibited by the density data in the Leschenault Estuary broadly parallel those recorded earlier in the Peel-Harvey Estuary (Potter *et al.* 1983), the prevalence of the 0+ age class between mid-winter and early spring was greater in samples collected from the latter system. This difference can be attributed to the fact that most of the crabs caught in the Peel-Harvey Estuary during that period were obtained from within the 5 km long entrance channel, where salinities almost invariably remained relatively high *i.e.* > 25 ppt, whereas such high salinities did not persist in Leschenault Estuary during winter. Moreover, crabs were no longer caught between mid-winter and early spring in either the saline river or more distal basin regions of the Peel-Harvey Estuary where, during that period, salinities typically decline to less than 10 ppt. This provides strong circumstantial evidence that the marked declines in salinity which occur in Leschenault Estuary during winter are likely to be the major factor initiating the emigration of crabs from this estuary at that time. However, it is also relevant that, during that period, some 0+ crabs do remain in Leschenault Estuary, whereas the vast majority of 1+ crabs leave that estuary. This suggests that 1+ crabs are even more sensitive than 0+ crabs to any marked declines in salinity.

Spawning period and location

The fact that the vast majority of the ovigerous females of *P. pelagicus* that were caught in Koombana Bay were collected between October and January provide strong evidence that this species spawns in this embayment during these months. Such a conclusion is consistent with the presence of large numbers of *P. pelagicus* zoea in plankton tows carried out by Le Provost *et al.* (1983) in Koombana Bay in mid to late November of 1982. The prevalence of ovigerous females of *P. pelagicus* is also greatest in late spring to mid-summer in Cockburn Sound (Penn 1977), a marine embayment to the north of Koombana Bay (Fig 1), and *P. pelagicus* zoea were abundant in plankton samples collected in Cockburn Sound during summer (Penn 1977). Thus, the main spawning period in Cockburn Sound is essentially the same as in Koombana Bay. Since female crabs in temperate waters remain ovigerous for about three weeks (Yatsuka 1962) and the abundance of ovigerous female crabs in Koombana Bay peaked in December, the presumptive zoea would typically be released into the water in January. Furthermore, the contrast between the abundance of crab zoea in samples collected in Koombana Bay and their absence or paucity in those obtained using the same methods in Leschenault Estuary (Meagher 1971; Anon 1983) provides strong circumstantial evidence that *P. pelagicus* typically spawns within the bay rather than the estuary.

The month when the number and prevalence of ovigerous females in Koombana Bay peaked, *i.e.* December and November respectively, was one month and two months earlier respectively, than was the case in Leschenault Estuary. The prevalence of ovigerous females in the Peel-Harvey Estuary, just to the north of the Leschenault Estuary (Fig 1), peaked in January and February (Potter *et al.* 1983), *i.e.* during a similar period as in the Leschenault Estuary. The earlier peak in ovigerous females in Koombana Bay than Leschenault Estuary can be related to the fact that large females, *i.e.* those belonging to the 1+ age class, remain in Koombana Bay during spring and early summer and are thus at a size and stage in maturity that enables them to spawn as soon as environmental conditions provide the appropriate trigger. In contrast, crabs entering the Leschenault Estuary in spring belong predominantly to the 0+ age class and are thus of a far smaller size, with the result that a substantial proportion of crabs do not start attaining a size equivalent to the CW_{50} at first maturity until December. It is also evident that, on the basis of the same measure of effort, both the number and prevalence of ovigerous females during the spring and summer were far greater in Koombana Bay than in the estuary. During the initial part of this period, this could likewise reflect in part the presence of many 1+ female crabs in Koombana Bay but not Leschenault Estuary, and thus the far greater likelihood of mating occurring. However, it is also possible that it reflects a tendency for females to leave the estuary as soon as egg extrusion has

occurred and for those ovigerous females to remain for a period in Koombana Bay before releasing their fertilised eggs.

In the context of the movement of female crabs out of the estuary, it is relevant that, in otter trawl catches, the sex ratio of crabs with a CW < 90 mm was close to parity in both Leschenault Estuary and Koombana Bay, whereas with crabs with a CW > 90 mm, the proportion of females was less than males in the estuary but greater than for males in the bay. This implies that, once female crabs reach the size at which they become mature, they have a greater tendency to move out of the estuary into Koombana Bay than do males of comparable size. This conclusion is consistent with the fact that, in the crab pot catches which contained crabs exclusively with a CW > 90 mm, the ratio of females to males was also far greater in Koombana Bay than Leschenault Estuary. Indeed, the fact that, during spring and summer, the mean monthly GSIs for female crabs, which had undergone a pubertal moult, were far lower in Leschenault Estuary than in Koombana Bay suggests that some female crabs may even leave the estuary for the bay before ovarian development is very advanced. However, since several of the larger female crabs, that were caught in the estuary during late summer and autumn had undergone a pubertal moult, but did not contain full spermathecae and were not ovigerous, some female crabs do apparently return to the estuary after spawning.

Length and age at first maturity

The minimum and maximum size at which female *P. pelagicus* was first found to attain sexual maturity in Leschenault Estuary correspond to carapace widths of 94 and 122 mm, with the carapace width at which 50% of the female crabs first reach maturity being estimated as 97 mm. The corresponding CW_{50} for males was 84 mm. These values are very similar to those recorded for *P. pelagicus* in the Peel-Harvey Estuary (de Lestang & Potter, School of Biological Sciences and Biotechnology, Murdoch University, unpublished data) and in Karwar on the coast of India (Sukumaran & Neelakantan 1996b). Rather higher CW_{50}s of 106 and 96 mm at first maturity were recorded by Ingles & Braum (1989) for female and male *P. pelagicus* in the Philippines.

The CW_{50}s for female and male crabs lie well within the discrete size group that in mid summer corresponds to crabs that are approximately one year old. Indeed, since the vast majority of female crabs that were at the beginning of their second year of life had undergone a pubertal moult, most crabs probably spawn when they are one year old. This parallels the situation found with *P. pelagicus* in South Australia (Smith 1982) and Moreton Bay in Queensland (Sumpton *et al.* 1994).

Diet

The composition of the diet recorded for *P. pelagicus* in this study demonstrates that, in the Leschenault Estuary, this species feeds mainly on slow-moving or relatively sessile benthic macroinvertebrates, such as amphipods, polychaetes, and bivalve and gastropod molluscs, and to a limited extent also on slow-moving benthic teleosts such as gobies. This species can thus be regarded as a benthic carnivore, thereby paralleling the situation recorded both for *P. pelagicus* elsewhere (Williams 1982; Edgar 1990) and for

other portunids (*e.g.* Hill 1979; Freier & Gonzales-Gurriaran 1995). The calcareous material found in the stomachs of *P. pelagicus* in Leschenault Estuary would provide the calcium required for the development of the exoskeleton of this species (Williams 1982). The diet of large crabs differed from that of small crabs in that it contained relatively greater amounts of polychaetes and relatively smaller amounts of amphipods. This difference is presumably related to the influence of an increase in the size of the chela and muscle mass on the type of prey that is most susceptible to predation (Freier *et al.* 1996) and to the greater ability of larger crabs to ingest larger prey such as polychaetes.

Portunus pelagicus in the Leschenault Estuary

The data presented in this paper on both the monthly trends exhibited by the size composition and abundance of crabs in Leschenault Estuary and Koombana Bay, when considered in conjunction with the time of spawning, have elucidated the broad details of the way in which *P. pelagicus* uses the Leschenault Estuary. Thus, after *P. pelagicus* has spawned in Koombana Bay, predominantly between the middle of spring and middle of summer, small numbers of the resultant 0+ age class start to become recruited into Leschenault Estuary in late summer and autumn. The numbers of this cohort decline in winter as salinities (and also water temperatures) fall to their lowest level, but then increase markedly as salinity and water temperature start rising sharply in mid-spring. The members of this cohort subsequently undergo rapid growth and, as a consequence, they typically attain maturity in late spring and summer when they are about one year old. Although female crabs apparently leave the estuary and enter Koombana Bay prior to or after becoming ovigerous, the fact that female crabs, which had undergone a pubertal moult, were present in the estuary during late summer and autumn, indicates that some female crabs do return to the estuary soon after spawning. However, male crabs are present in relatively greater numbers in the estuary during the same period, which indicates that they exhibit a greater tendency to remain in the estuary during this period. The larger crabs *i.e.* those representing the 1+ age class, are found in Leschenault Estuary until May and June, by which time they are *ca* 1½ years old. However, the majority of these larger crabs subsequently leave the estuary as salinities and also water temperatures fall to low levels in winter and, unlike the representatives of the 0+ cohort, rarely return as these two environmental variables start rising in the middle of spring. The significantly greater size of female than male crabs in crab pots in Leschenault Inlet parallels the situation found with another portunid, *Scylla serrata*, in Queensland (Williams & Hill 1982). Finally, our data show that, during its time in the estuary, *P. pelagicus* feeds predominantly on macrobenthic invertebrates and occasionally bottom-living fish.

References

Anon 1983 Population dynamics of blue-manna crabs in Koombana Bay and Leschenault Inlet. Report by LeProvost I, Semeniuk V & Chalmer P, Environmental Consultants for the State Energy Commission, Perth, Western Australia.

Anon 1988 SPSS-X User's Guide. SPSS, Chicago

Edgar G J 1990 Predator-prey interactions in seagrass beds. II. Distribution and diet of the blue manna crab *Portunus pelagicus* Linnaeus at Cliff Head, Western Australia. Journal of Experimental Marine Biology and Ecology 139:23-32.

Freier J & Gonzáles-Gurriáran E 1995 Feeding ecology of the velvet swimming crab *Necora puber* in mussel raft areas of the Ri de Arousa (Galicia, NW Spain). Marine Ecology Progress Series 119:139-154.

Freier J, Paz Sampedro M & Gonzáles-Gurriáran E 1996 Influence of morphometry and biomechanics on diet selection in three portunid crabs. Marine Ecology Progress Series 137:111-121.

Hill B J 1979 Aspects of the feeding strategy of the predatory crab *Scylla serrata*. Marine Biology 55:209-214.

Hill B J 1980 Effects of temperature on feeding and activity of the crab *Scylla serrata*. Marine Biology 59:189-192.

Hynes H B N 1950 The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. Journal of Animal Ecology 19:36-58.

Hyslop E J 1980 Stomach contents analysis - a review of methods and their application. Journal of Fish Biology 17:411-429.

Ingles J & Braum E 1989 Reproduction and larval ecology of the blue swimming crab *Portunus pelagicus* in Ragay Gulf, Philippines. International Revue of Hydrobiology 74:471-490.

Jones D S & Morgan G J 1994 A Field Guide to Crustaceans of Australian Waters. Reed, Sydney.

Kailola P J, Williams M J, Stewart P C, Reichelt R E, McNee A & Grieve C 1993 Australian Fisheries Resources. Bureau of Resource Sciences, Department of Primary Industries and Energy, and the Fisheries Research and Development Corporation, Canberra.

Meagher T D 1971 Ecology of the Crab *Portunus pelagicus* (Crustacea: Portunidae) in South Western Australia. PhD Thesis, Department of Zoology, University of Western Australia.

Penn J W 1977 Trawl-caught fish and crustaceans from Cockburn Sound. Report 20. Department of Fisheries and Wildlife Western Australia, Perth.

Potter I C, Chrystal P J & Loneragan N R 1983 The biology of the blue manna crab *Portunus pelagicus* in an Australian estuary. Marine Biology 78:75-85.

Reeby J, Prasad P N & Kusuma M S 1990 Size at maturity in the male crabs of *Portunus sanguinolentus* and *P. pelagicus*. Fishery Technology 27:115-119.

Saila S B, Recksieck C W & Prager M H 1988 Basic Fisheries Science Programs. Elsevier, New York.

Semeniuk V & Meagher T D 1981 The geomorphology and surface processes of the Australind-Leschenault Inlet coastal area. Journal of the Royal Society of Western Australia 64:33-51.

Smith H 1982 Blue crabs in South Australia - their status, potential and biology. Safic 6:6-9.

Somerton D A & Donaldson W 1996 Contribution to the biology of the grooved and triangle tanner crabs, *Chionoecetes tanneri* and *C. angulatus*, in the eastern Bering Sea. Fishery Bulletin 94:348-357.

Stephenson W 1962 Evolution and ecology of portunid crabs, with especial reference to Australian species. In: The Evolution of Living Organisms (ed G W Leeper). Melbourne University Press, Melbourne, 311-327.

Sukumaran K K & Neelakantan B 1996a Mortality and stock assessment of two marine portunid crabs, *Portunus (Portunus) sanguinolentus* (Herbst) and *Portunus (Portunus) pelagicus* (Linnaeus) along the south-west coast of India. Indian Journal of Fisheries 43:225-240.

Sukumaran K K & Neelakantan B 1996b Relative growth and sexual maturity in the marine crabs, *Portunus (Portunus) sanguinolentus* (Herbst) and *Portunus (Portunus pelagicus* (Linnaeus) along the south west coast of India. Indian Journal of Fisheries 43:215-223.

Sumpton W D & Smith G S 1990 Effect of temperature on the emergence, activity and feeding of male and female sand crabs (*Portunus pelagicus*). Australian Journal of Marine and Freshwater Research 41:545-550.

Sumpton W D, Potter M A & Smith G S 1989 The commercial pot and trawl fisheries for sand crabs (*Portunus pelagicus*) in Moreton Bay, Queensland. Proceedings of the Royal Society of Queensland 100:89-100.

Sumpton W D, Potter M A & Smith G S 1994 Reproduction and growth of the commercial sand crab *Portunus pelagicus* (L.) in Moreton Bay, Queensland. Asian Fisheries Science 7:103-113.

Van Engel W A 1958 The blue crab and its fishery in Chesapeake Bay. Part 1. Reproduction, early development, growth and migration. Commercial Fisheries Review 20:6-17.

Warner G F 1977 The Biology of Crabs. Paul Elek Scientific Books, London.

Williams M J 1982 Natural food and feeding in the commercial sand crab *Portunus pelagicus* Linnaeus, 1766 (Crustacea: Decapoda: Portunidae) in Moreton Bay, Queensland. Journal of Experimental Marine Biology and Ecology 59:165-176.

Williams M J & Hill B J 1982 Factors influencing pot catches and population estimates of the portunid crab *Scylla serrata*. Marine Biology 71:187-192.

Yatsuka K 1962 Studies on the artificial rearing of the Brachyura, especially of the larval blue crab *Neptunus pelagicus* (L). Report of the USA Biological Station 9:12-13.